River bank burrowing by invasive crayfish:
Spatial distribution, biophysical controls and biogeomorphic significance

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ABSTRACT

Invasive species generate significant global environmental and economic costs and represent a particularly potent threat to freshwater systems. The biogeomorphic impacts of invasive aquatic and riparian species on river processes and landforms remain largely unquantified, but have the potential to generate significant sediment management issues within invaded catchments. Several species of invasive (non-native) crayfish are known to burrow into river banks and visual evidence of river bank damage is generating public concern and media attention. Despite this, there is a paucity of understanding of burrow distribution, biophysical controls and the potential significance of this problem beyond a small number of local studies at heavily impacted sites. This paper presents the first multi-catchment analysis of this phenomenon, combining existing data on biophysical river properties and invasive crayfish observations with purpose-designed field surveys across

103 river reaches to derive key trends. Crayfish burrows were observed on the majority of reaches, but burrowing tended to be patchy in spatial distribution, concentrated in a small proportion (<10%) of the length of rivers surveyed. Burrow distribution was better explained by local bank biophysical properties than by reach-scale properties, and burrowed banks were more likely to be characterised by cohesive bank material, steeper bank profiles with large areas of bare bank face, often on outer bend locations. Burrow excavation alone has delivered a considerable amount of sediment to invaded river systems in the surveyed sites (3 t km^{-1} impacted bank) and this represents a minimum contribution but certainly an underestimate of the absolute yield (submerged burrows were not recorded). Furthermore, burrowing was associated with bank profiles that were either actively eroding or exposed to fluvial action and/or mass failure processes, providing the first quantitative evidence that invasive crayfish may cause or accelerate river bank instability and erosion in invaded catchments beyond the scale of individual burrows.

KEYWORDS: invasive species, ecosystem engineer, biogeomorphology, bank erosion, sediment dynamics, signal crayfish

HIGHLIGHTS

- The impacts of invasive species on river morphology remain largely unquantified
- We analysed the spatial distribution and impact of signal crayfish on river banks
- Burrows were associated with steep, bare banks and indicators of bank erosion
- Excavation of (visible) burrows delivered on average 3 t km^{-1} burrowed river bank

1. INTRODUCTION

Invasive species are one of the most important drivers of biodiversity loss and ecosystem service change at the global scale (Millennium Ecosystem Assessment, 2005; Simberloff *et al.*, 2013; Cameron *et al.*, 2016; Gallardo et al., 2016), generating estimated economic damages of up to 5% of the global economy (Pimental *et al.*, 2001) and £1.7 Billion in Britain alone (Williams *et al.*, 2010). Recent international legislation on Invasive Alien Species (European Parliament, 2014) requires advancement of the scientific evidence base for invasive species and their impacts in order to inform risk assessment and mitigation. Freshwater environments are biodiverse and highly invasible, exposing them to disproportionately severe impacts from invasive species (Moorhouse and Macdonald, 2015a). Despite this, and the increasing recognition of the importance of reciprocal biotic-abiotic interactions, ecosystem engineering and the geomorphic agency of (native) biota (e.g. Moore, 2006; Corenblit *et al.*, 2011; Rice *et al.*, 2012) the link between geomorphic processes and invasive species has been largely overlooked, with significant implications for environmental management (Fei *et al.*, 2014).

Biogeomorphic impacts of invasive species include bioturbation, bioerosion and bioconstruction (Fei *et al.*, 2014) and traits, such as tolerance of varied environmental conditions, that make introduced aquatic species attractive for aquaculture (Peay, 2010) and in some cases the aquarium trade (Maceda-Veiga et al., 2013) mean that species and their impacts may rapidly become widespread. Known impacts in aquatic environments are numerous (DAISIE European Invasive Species Gateway, 2008), but examples include changes to suspended particulate material through bioturbation and excretion by invasive non-native fish (Matsuzaki *et al.*, 2007) and potential contributions to soil erosion and sediment delivery through winter die-back of invasive riparian plants (e.g. *Impatiens glandulifera*; Greenwood and Kuhn, 2014). Larger freshwater invertebrates such as invasive non-native crayfish have also been shown to significantly alter bed topography and roughness (Johnson *et al.*, 2010), increase gravel transport (Johnson *et al.*, 2011) and generate pulses of fine sediment mobilisation sufficient to drive an increase in suspended sediment concentrations (Harvey *et al.*, 2014; Rice *et al.*, 2014) through their interactions with the river bed (e.g. movement and creation of pit and mound structures).

Several species of invasive non-native crayfish are known to dig burrows into river banks, including spiny cheek crayfish (*Orconectes limosus*), virile crayfish (*Orconectes virilis*), red swamp crayfish (*Procambarus clarkii*) and signal crayfish (*Pacifastacus leniusculus)*. Of these, *P. leniusculus* is by far the most widespread invader in Europe (Johnsen and Taugbol, 2010), known to inhabit a wide range of freshwater environments (Ruokonen *et al.*, 2012) and achieve densities of up to 20 individuals m^{-2} (Abrahamsson and Goldman, 1970; Bubb *et al.*, 2004). Field observations have linked crayfish burrowing with accelerated bank erosion and increased fine sediment delivery (Guan, 1994; Holdich, 1999; Angeler *et al.*, 2001) and Harvey *et al.* (2011) hypothesised that river bank burrowing by *P. leniusculus* may contribute to bank erosion and sediment delivery in two ways: directly through the mechanistic displacement of sediment generated by burrow excavation; and indirectly through the geotechnical effects of burrow networks on bank stability and hence susceptibility to fluvial, subaerial and mass failure processes.

River sites with evidence of intensive burrowing activity have attracted media attention, raising concerns about bank collapse, flood risk and footpath erosion (e.g. Fairhall, 2002; Eccleston, 2008) and control measures such as manual trapping are incapable of eradicating populations from infested reaches (Moorhouse and Macdonald, 2015b). Despite this, little is known of the spatial extent and distribution of burrowing which in some cases (e.g. *P. leniusculus*) represents a trait apparently unique to invaded environments (Guan, 1994; Holdich, 1999). The majority of information to date is based on local studies of heavily impacted sites (e.g. Guan, 1994; Stanton, 2004) and there remains a deficiency of information on the spatial distribution, controls and potential significance of this biogeomorphic impact. This paper addresses this important knowledge gap, providing the first extensive 'large-N' multi-catchment approach (Richards, 1996) and combining existing publicly available data with bespoke field survey for a large number of UK river reaches in order to identify key trends. The paper addresses four specific research questions:

1. How spatially widespread and locally intensive is invasive (non-native) crayfish bank burrowing within invaded catchments?

2. To what extent can the occurrence of invasive crayfish bank burrowing be explained by biophysical river properties at the reach or bank section scale?

3. How much sediment has been excavated from river banks due to invasive crayfish burrowing within impacted river reaches?

4. Is there a link between invasive crayfish burrowing and river bank erosion beyond the scale of individual burrows?

2. MATERIALS AND METHODS

2.1 Research design and field sites

The research focused on seven rivers within the wider River Thames catchment, UK. This large (16,000 km^2) catchment includes 38 main tributaries and contains the most densely populated urban areas in the UK as well as Areas of Outstanding Natural Beauty. The seven rivers selected for study are predominantly lowland, low energy rivers (altitude <83 m AOD; slope <0.001) underlain by chalk, sandstone, limestone and clay (BGS, 2016). They achieve good geographic coverage of the wider Thames catchment (Figure 1) and are representative of the high proportion of lowland, low energy rivers in the UK (Jeffers, 1998; Harvey *et al.*, 2008).

The analysis combined existing data sets with new data from purpose-designed field surveys. Field sites were selected using the Environment Agency's River Habitat Survey database (Raven *et al.*, 1998) which represents the most comprehensive UK data resource documenting river biophysical properties (sediment, vegetation, morphology) at the scale of 500m long river 'reaches'. The National Biodiversity Network Gateway (NBN, 2015) was used to verify that burrowing invasive crayfish (all non-native and hereafter referred to as invasive crayfish for brevity) have been recorded in the vicinity of each field site, using observations of presence either adjacent to the RHS reach or upstream and downstream. NBN records show that *P. leniusculus* is widely distributed across the surveyed catchments (Figure 1), but there were only three observations of *O. virilis* (River Lee), no observations of *O. limosus*, and *P. clarkii* are limited to Hampstead Heath and Regents Canal. *P. leniusculus* are therefore likely to account for the vast majority of invasive burrowing crayfish in the Thames catchment (see also Almeida *et al.*, 2014), but it is possible that at some reaches other burrowing invasive crayfish may be present. While the use of the NBN data resource does not guarantee invasive crayfish presence at the surveyed reaches at the time of survey or provide population density estimates, it is the best evidence available at this extensive spatial scale to indicate that invasive crayfish are present in the reach or have been in the recent past. Observations for surveyed sites date back to 1978, and precision ranges between 100m and 10km but the majority of observations along surveyed rivers were recorded since 2000 (68%) and accurate to at least 1km (98%). For each of the seven rivers, a stratified random sampling design was applied to reaches with available RHS data and positive NBN records. A total of 14 or 15 reaches were selected on each river, ensuring that coverage was spread across the upstream, mid and downstream sections of each river.

2.2 Crayfish burrow survey

Crayfish burrows have a characteristic flattened ‘D’ shape whereby the bottom of the chamber is flat. This, together with the absence of features associated with other species such as water voles or rats (e.g. platforms, latrines, feeding signs) allows them to be identified visually in the field. Field surveyors had extensive field experience of native and non-native crayfish research. For each reach (n = 103), the presence and abundance of burrows was recorded through visual observation from the channel or opposite bank in either Autumn 2013 or Spring 2014, when vegetation cover was relatively sparse and under low flow conditions as recommended for RHS (Environment Agency, 2003). A survey of the 500 m long RHS reach was attempted at all sites, but for some reaches, bank and channel access limited the length of bank face along which burrows could be observed. As a result, the maximum accessible bank length was surveyed and recorded for each reach (and this ranged between 70 m and 800 m). To minimise uncertainties in observations of burrows submerged at the time of survey due to water turbidity and depth, only burrows above the (low flow) water surface at the time of survey were recorded. The number of burrows observed is therefore certainly an underestimate of the total number of burrows present, but was used to identify spatial distribution and local intensity. At each reach, burrow presence/absence was recorded, and for reaches where burrows were observed, the total number of burrows observable and the total length of bank impacted by burrowing was recorded (combining left and right banks). To account for variability in the length of reach surveyed for burrows, impacted bank length is presented as a percentage of surveyed bank length in a similar manner to other survey approaches where reach length may vary (Gurnell *et al.*, 2014).

In addition to the reach scale survey, for each reach where at least one burrow was observed (n = 69; Figure 1a) detailed recordings were made for individual ‘bank sections’. Each bank section comprises a 10 m long stretch of bank and adjacent channel. To maximise accuracy of observations, bank sections were surveyed only where a good view of the bank face was possible. At each reach, a maximum of 20 bank sections were selected for detailed survey. Bank sections were chosen to achieve approximately equal spacing along the reach and to include up to 10 bank sections with burrows (but fewer where burrows occurred over a short length of the reach). The median number of bank sections surveyed per reach was 10, with a range of 4 - 20 (Fig. 1b). Overall, the dataset included 768 bank sections across the 69 reaches that contained at least one observed burrow. Three burrow variables were recorded for each bank section: burrow presence/absence, the total number of burrows (above the water surface) and the length of bank impacted by burrows (to the nearest 1m). A linear burrow density was then calculated as the number of burrows divided by the impacted bank length.

2.3 Reach scale biophysical indices

RHS provides a standard field method for recording the physical character of rivers along 500m 'reaches' through visual assessment and simple measurements of channel dimensions (Environment Agency, 2003). The method has been applied across the UK to produce a large database (> 24,000 reaches) of biophysical river properties (River Habitat Survey, 2012). The survey records observations of channel and bank features (e.g. sediment calibre, vegetation types, geomorphological features) at ten equally spaced 'spot-check' transects, together with a 'sweep-up' component designed to capture the general river characteristics (including land use with 50 m of the bank top, bank profiles, artificial structures, major impacts and nuisance plant species) and infrequent channel, bank and riparian vegetation features not occurring at spot-checks (Environment Agency, 2003). The method captures more than 200 compulsory data entries per site, largely in the form of presence, absence and extent of features (River Habitat Survey, 2012). In order to summarise reach-scale biophysical properties and make effective use of categorical data, RHS-derived indices have been successfully applied to explore catchment controls on sequences of geomorphic units (Emery *et al.*, 2004), to classify the biophysical characteristics of urban rivers (Davenport *et al.*, 2004) and to investigate relationships between physical habitat and lithology (Harvey *et al.*, 2008).

Six landscape scale indices (providing contextual information on reach position within the catchment, channel dimensions and energy environment) and nine reach scale indices (providing information on instream and riparian vegetation, and bed and bank material calibre and surface flow types) were derived from the RHS database (Emery *et al.*, 2004; Harvey *et al.*, 2008; Table 1). The FLOW index was created to summarise the occurrence of different flow conditions, with lower values indicating a higher frequency of slower, and less hydraulically ‘rough’ flow types. Likewise, there was no pre-existing index to summarise bank profile data, which was considered of potential importance to bank burrowing by invasive crayfish. An additional index was created (BANKPROF) to indicate availability of shallower or steeper bank profiles using the bank profile information recorded as part of the ‘sweep up’ component of RHS (Table 1). Each type of bank profile is recorded as absent (<1%), present (<33%) or extensive (>=33%) along the full 500 m RHS reach. Bank profile types are vertical/ undercut (including eroding and stable cliffs), vertical with toe (i.e. slumped material at the base), steep (Bank slope >= 45% but not predominantly vertical), gentle (bank slope < 45%), composite (complex profile caused by previous slumping/erosion) and natural berms. Bank types were scored to reflect increasing steepness of the bank face at the channel edge (Table 1). Two summary indices can also be calculated from RHS data: a Habitat Modification Score (HMS) which represents the level of anthropogenic disturbance to the river channel and surrounding corridor and a Habitat Quality Assessment (HQA) score based on features considered to be of importance to wildlife, and these were included in this analysis. Although some channel and bank features are used to create sub-scores for the RHS Habitat Quality Index (HQA), these focus on the diversity of features and not the type of river environment. As a result, the overall HQA score was used to indicate the quality and diversity of habitat features, and a range of more detailed indices were computed to describe the type river environment for each reach (Table 1).

2.4 Bank section scale biophysical indices and erosion indicators

A field survey of biophysical properties was undertaken at the bank section scale in order to provide a higher resolution data set of bank properties at locations with and without burrows. Variables were collected for each bank section and adjacent channel area based on modification of the RHS (Environment Agency, 2003) and Urban River Survey (Gurnell *et al.*, 2014) methods. Key variables related to bank characteristics were recorded including bank angle, planar angle (position in relation to channel planform), exposed bank height, bank substrate and % cover of different vegetation types on the bank face and bank top (Table 2). Bank material was coded as either artificial (1), non-cohesive (2) or cohesive (3; combining earth and clay), with the coding reflecting increasing ease of burrowing. Bank vegetation data incorporates greater detail than traditional RHS surveys to address potential implications for bank stability such as different root structures. In additional, channel characteristics adjacent to the bank section were recorded (channel width/depth, surface flow types, availability of substrate and other types of cover (wood, boulders) and channel vegetation types; see Table 2), although water turbidity limited the capture of these data at many transects.

Since RHS does not explicitly include indicators of river bank erosion, presence of erosion and the length of bank impacted (m) were recorded at each bank section following Thorne (1998). This involved visual identification of features associated with bank retreat caused by fluvial erosion and/or mass failure. These included undercut sections of bank and exposed tree roots which result from the detachment and entrainment of bank material due to lift and drag forces exerted by flow (Figure 2a), and the presence of cracks and blocks of failed material in the bank toe region caused by the collapse and movement of bank material under gravity (Figure 2b; Thorne, 1982).

2.5 Estimation volume of sediment excavated from burrowing

Crayfish burrow abundance at the reach scale was used in combination with data on burrow dimensions to estimate the volume of material excavated from the reaches where burrows were observed. Average burrow dimensions (length 0.2m, burrow entrance widths 0.1 m and height of 0.08 m) were applied universally across the reaches, based on previous research within the Thames catchment (Roberts, 2012) which are comparable with observations elsewhere (Stanton, 2004), assuming a single chamber straight burrow morphology with a single opening. Burrow architecture can vary considerably from single straight chambers to branched networks with multiple openings although single straight chambers have been identified as the most common (Guan, 1994; Stanton, 2004). The assumption of a single straight chamber therefore represents a conservative approach to burrow volume calculation. Burrow volume was calculated as the volume of an elliptical cylinder (Eq. (1): burrow volume calculation).

$$Burrow\ volume = \pi ABL/4$$

Where A = major axis (entrance width), B = minor axis (entrance height) and L = length.

Equation 1: Burrow volume calculation based on elliptical cylinder

2.6 Data Analysis

The majority of variables (reach and bank section scale) were not normally distributed (Kolmogorov-Smirnov p <0.05) and therefore non-parametric tests were used to analyse the data sets. Differences between groups were explored using Mann Whitney U test (2 groups) or Kruskall Wallis H test with post-hoc tests (>2 groups) and bivariate correlations were assessed using Spearman's Rank tests. Principal Component Analysis (PCA) was applied to derive the dominant environmental gradients in the reach and bank section survey data based on a Spearman's rho correlation matrix with orthogonal rotation (Varimax with Kaiser normalisation). Correlations between pairs of independent variables were scrutinized prior to PCA, leading to the removal of site altitude and TSPI (Total Stream Power Index) from the reach scale analysis due to their high correlations with Slope (ρ = 0.762) and CSA (cross sectional area; ρ = 0.812), respectively. Bartlett's test of sphericity ($X^2 = 140.9, p < 0.0001$ for the reach scale analysis and $X^2 = 6926.0, p < 0.0001$ for the bank section scale analysis) indicated that correlations between the remaining pairs of independent variables were sufficiently large for PCA. Presence/absence of crayfish burrows were related to the extracted principal components at the reach and bank section scale, respectively, using generalized linear models (multiple logistic regression using a logit link and binomial error distribution). Backward stepwise elimination (likelihood ratio) was used to select principal components for inclusion in the final models. Cross-tabulation and Chi square tests were performed to assess associations between burrowing presence/absence and erosion presence/absence. Analyses were performed in XLSTAT-Base (2016) and SPSS (v. 22).

3. RESULTS

3.1 Catchment-scale spatial distribution and local intensity of burrowing

In total, 29 km of river banks were surveyed across 103 reaches on the seven rivers. Key burrow metrics are presented in Table 3 and Figure 3. The surveyed lengths varied between 70m and 800m (median 270m), as at no reach was it possible to accurately visually assess burrow presence along all 500m of left and right banks due to restricted access to the banks or channel. Crayfish burrows were recorded on 69 (67%) of the 103 surveyed reaches and on the majority (60-93%) of reaches for all of the individual rivers with the exception of the River Colne which had the lowest number of reaches with observed burrows (3 out of 15 reaches; Figure 3). The Mole and Loddon rivers had the highest proportion of reaches with burrows and the Kennet, Lee, Wey and Windrush rivers had a similar proportion of burrowed reaches (60-73%).

The number of burrows recorded ranged from 1 to 87 per reach (median = 12) and the proportion of surveyed bank with observed burrows ranged from 0.2% to 23.5% (median = 3.2%; Figure 3a) indicating a patchy distribution of burrows concentrated in certain parts of the surveyed reaches. For all reaches where at least one burrow was observed, a total of 5% of the surveyed bank length contained burrows but there was considerable variability among rivers (Figure 3b). The proportion of bank length impacted by burrows was more variable on the Kennet, Lee and Windrush, suggesting high variability in burrowing on a reach-by-basis including some heavily impacted sites (>=15% impacted bank length), while the Mole and Wey had lower median values and less variability between reaches. There were no statistically significant differences in impacted bank length between rivers (Kruskall

Wallis $p > 0.05$) and no statistically significant correlations between distance downstream and the impacted bank length or burrow density on individual rivers (Spearman's Rank $p > 0.05$) suggesting an absence of longitudinal trends.

The more detailed survey of individual bank sections within reaches where at least one burrow was observed captured information for n = 245 bank sections with burrows. A total of 881 burrows were recorded across the 245 bank sections with a median of 3 burrows per section and a maximum of 16 (Table 3). The majority of bank sections with burrows had < 6 burrows per bank section, < 5m of impacted bank length (median = 2m) and a linear density of <3 burrows per m length of bank, with a small minority of transects associated with higher burrow densities of up to a maximum of 6 per m of impacted bank length. The seven rivers revealed differences in the three burrowing metrics (Figures 3c, d, e), with higher numbers of burrows and longer impacted lengths on the rivers Windrush, Kennet and Lee, compared to the Mole, Colne and Loddon. The Wey represents a slight anomaly since it was associated with lower numbers of burrows but some longer impacted lengths. The distribution of burrow densities showed greater similarity across the rivers although the Windrush was associated with a higher median (2) and the Colne and Lee showed narrower ranges of (lower) density values compared to the other rivers. Kruskall Wallis post-hoc tests revealed significantly greater numbers of burrows and longer impacted bank lengths on the Windrush compared to the Wey, Loddon and Mole, and significantly higher burrow density on the Windrush compared to the Wey, Loddon and Lee ($p < 0.05$).

3.2 Relationships between burrowing and biophysical river habitat characteristics at the reach and bank section scale

All of the reach-scale RHS-derived indices showed considerable overlap in values between reaches with and without burrows, but statistically significant differences between burrowed and non-burrowed reaches were identified for three indices. Reaches with observed burrows were associated with larger channels (higher CSA; Mann-Whitney U $p < 0.05$), greater availability of steeper bank profiles (higher BANKPROF, Mann Whitney U $p < 0.05$) and higher habitat quality (HQA, Mann Whitney U $p < 0.10$) when compared to non-burrowed sites (Figure 4). Principal Components Analysis (PCA) was performed on the RHS-derived variables. Five principal components (PCs) with eigenvalues >1 and were initially identified but inspection of the scree plot revealed a clear inflexion point which indicated that only the first two components should be retained for further analysis.. Variable loadings are presented in Table 4. Together, these PCs explained 39.9% of the variance and were interpreted to represent key gradients in river energy and channel size (PC1), and habitat quality/modification, riparian vegetation complexity and bank morphology and material (PC2). No significant difference in PC scores was detected between burrowed and non-burrowed reaches (Mann Whitney U $p > 0.01$ for PC1 and PC2) and the reach scale logistic regression model was not statistically significant ($X^2 = 3.02,\ p = 0.082$).

The detailed biophysical habitat characteristics sampled at the bank section scale were also assessed for bank sections with and without burrows (n = 69 sites; 768 bank sections and 245 with burrows). Given the difficulties identifying channel substrate and submerged vegetation types at many sites due to high turbidity levels, analysis focused on bank-related variables. Burrowed sections were associated with wider channels and burrows were almost exclusively found on banks with cohesive bank material: 99% cohesive, 1% non-cohesive, compared to 96% cohesive, 3% non-cohesive and 1% artificial for sections without burrows. Burrowed sections were also associated with significantly higher bank angles, larger areas of bare bank face, lower bank face coverage of emergent narrow leaved and broad leaved vegetation, grass, herbaceous vegetation and trees, and wider channels (Mann Whitney U$p<0.05$; selected examples in Figure 4).

The first six PCs had eigenvalues greater than 1 and detailed inspection of the scree plot confirmed a clear inflexion point following the sixth component. Together, the six PCs explained 62% of the variance in the data. The PC loadings (Table 4) were used to interpret the gradients represented by the PCs. PC1 defines a gradient of bank vegetation type (from grasses to herbaceous vegetation) on the bank face and top while PC2 describes gradient of decreasing availability of bare substrate at the bank face (and increasing grass cover), and increasing cover of emergent vegetation at the bank toe (indicative of lower flow velocities). PC3 represents a gradient of increasing channel size and PC4 represents increasing coverage of taller vegetation at the bank top. PC5 represents a gradient of increasing bank height and presence of taller vegetation on the bank face. PC6 is a bank profile gradient, with higher PC scores representing steeper banks on outer bends (cliffs) with low bank face tree coverage and lower scores representing shallow sloping banks on the inside of bends. Mann Whitney U tests revealed statistically significant differences ($p < 0.001$) between sections with and without burrows for PCs 2 and 6 (Figure 5). The bank section scale logistic regression model was constructed using five of the six principal components (Table 5). The model was statistically significant ($X^2 = 111.593,\ p < 0.0001$) and explained 21% of the observed variance in crayfish burrow presence at the bank section scale (Nagelkerke R^2). PCs 2 and 6 were found to be the most important predictors of crayfish burrowing, with steeper bank profiles on outer bend locations (higher scores on PC6) and greater availability of bare bank with a lack of vegetation cover at the bank toe (lower scores on PC2) associated with an increased likelihood of crayfish burrow presence.

3.3 Estimated volume of sediment excavated due to burrowing

The estimated volumes of bank material excavated through burrow creation are presented in Table 6. In total, invasive crayfish burrowing has delivered a *minimum* of 1876L of bank material from the 29 km of surveyed river stretches. The amount of material excavated from individual rivers ranged from a minimum of 59L on the River Colne to a maximum of 446L on the Windrush. On average across the seven rivers, approximately 2L of sediment was excavated per metre of impacted bank length. Assuming an average soil bulk density of 1.5g/cm^3 this equates to an average sediment yield of 3 t km^{-1} for burrowed sections.

3.4 Relationships between crayfish burrowing and indicators of bank erosion

A total of 261 out of 768 bank sections (34%) exhibited features indicative of bank erosion. The length of bank impacted by erosion was generally short (92% < 5m; 50% surveyed bank section) with a smaller number of bank sections (15) with erosion recorded across 8-10m within the 10m long bank sections. The PC scores derived from biophysical habitat properties were used to explore the grouping of erosion features along the principal environmental gradients in the data set. Bank sections with erosion show a similar pattern in PC scores for PCs 2-6 to the bank sections with crayfish burrows present (see Figure 5) and Mann Whitney U Tests confirm significant differences between sections with and without erosion present for PCs 2, 4 and 6 ($p < 0.05$). Bank sections with erosion indicators were associated with steeper bank profiles on outer bend locations (higher scores on PC6), greater availability of bare substrate with a lack of vegetation cover at the bank toe (lower scores on PC2), and low coverage of tall vegetation at the bank top (low scores on PC4).

Cross-tabulation between the nominal variables “burrow presence/absence” and “erosion presence/absence” was used to explore the co-occurrence of burrowing and erosion. Where burrows were absent, erosion was absent at the majority of bank sections (77.5%) and present at 22.5% of bank sections. In contrast, where burrows were present, erosion was present on the majority of bank sections (59%) and absent from 41%. The Chi-square statistic was significant ($p < 0.01$), confirming a significant association between the frequency of burrowing and frequency of features indicative of river bank erosion beyond the scale of individual burrows. Phi and Cramer’s V coefficients, providing measures of association between the two categorical variables, indicated a weak (0.357) but statistically significant ($p < 0.01$) positive correlation between presence of burrows and presence of erosion.

5. DISCUSSION

Our results provide an important contribution to the understanding of the impacts of invasive species on river morphology. Crayfish burrows were observed on the majority (67%) of surveyed reaches and the frequency of burrow presence was relatively similar across rivers, illustrating that burrowing is widespread. In contrast, the percentage of bank length impacted by burrows and the density of burrows was more variable across reaches and rivers and generally patchy in distribution.. The (linear) burrow density was 3 burrows m^{-1} bank length or less for the majority of bank sections, but a small number of sections showed higher intensities of burrowing (up to 6 burrows m^{-1} bank length). However, since visual observations excluded burrows beneath the water surface at the time of survey, these figures represent a significant underestimate of total burrow presence. For example, submerged burrow densities of 0.47 – 9.0 m^{-1} have been identified on rivers in Buckinghamshire and Leicestershire, with larger numbers of burrows identified below the water surface at the time of survey (Guan, 1994; Stanton, 2004). Our field observations indicated a larger proportion of burrows above the water surface under low flow conditions at some reaches but irrespective of this, the density figures inevitably underestimate the total burrow occurrence and density.

At the reach-scale, exploratory analysis indicated that burrow presence was associated with larger channels, greater availability of steep bank profiles and higher habitat quality (HQA) scores. The potential relationship with HQA suggests that reaches with higher habitat quality may be at greater risk from potential negative impacts from crayfish burrowing (e.g. sedimentation of habitats). Interestingly, this finding is inconsistent with the general perception that degraded habitats are more susceptible to invasive species (Sandlund et al., 2001; Natural England, 2015). It may reflect an increased presence of eroding bank habitats within semi-natural rivers in comparison to modified river channels, and warrants further investigation given the potential implications for compliance with legislation such as the EU Water Framework Directive (WFD; European Parliament, 2000). The bank profile index indicates that local scale biophysical properties may be more important in explaining the occurrence of crayfish burrows and this is supported by the purpose-designed field survey undertaken at the bank section scale. At the bank section scale, burrow presence was associated with certain types of banks: those with cohesive bank material, steeper bank profiles banks, a high proportion of bare bank face, low vegetation cover at the bank toe and outer bend locations (Figure 6). Burrowing has traditionally been considered an energy expensive process (Meysman *et al.* 2006) and these bank profiles may offer greater ease of burrowing which may be particularly important where other forms of shelter (e.g. vegetation) are limited. Given that other factors such as population size, competition, predation and availability of alternative shelter are also likely to influence burrowing behaviour (Stanton, 2004), the influence of local bank properties appears relatively strong.

The types of bank associated with burrowing also display indicators of bank erosion beyond the scale of individual burrows. While it is not possible to assign causality to this relationship on the basis of this data set alone, this link is critical. Even if these locations were already subject to erosion through fluvial and mass failure processes, there is strong theoretical justification for accelerated bank retreat arising from the interaction between bank face cavities and near-bank flow (Ozalp *et al.*, 2010; Jackson *et al.*, 2015), and changes to bank hydrology leading to mass failure (Fox and Wilson, 2010). On the basis that crayfish burrows have a typical length of 0.2 m and the median bank height across the study reaches is 1.0 m, up to 375 m^3 of river bank (equivalent to 563 t of sediment) is potentially at risk of being undermined by the presence of crayfish burrows across the surveyed sites. The explorative nature of the survey excludes any quantitative analysis of erosion rates and includes ‘dormant’ as well as actively eroding bank sections (Thorne, 1998), but the results provide strong justification for further research to characterise and quantify the interactions between crayfish burrowing and geotechnical bank failure, and to explore why crayfish burrow in certain conditions in order to help predict impacts.

Aside from contributions to geotechnical bank failure, however, our data show that through the direct mechanistic activity of digging burrows into river banks, invasive crayfish have excavated and delivered to the river network an average of 3 t km^{-1} in impacted sections since invasion, based on visible burrows. The total volume of sediment delivered via this mechanism will be considerably higher as a result of un-surveyed submerged burrows and the occurrence of more complex burrow architectures. Furthermore, since burrows tend to occur on exposed or eroding banks, it is likely that repeat phases of burrow excavation may occur following bank collapse. Computation of a precise yield and any temporal patterns would require further more detailed and spatially extensive field survey, sediment sampling and accurate timescales for the passing of invasion fronts, data which are either highly labour-intensive on this scale, or unavailable. However, this material represents a considerable additional input of fine sediment to the channel network since invasion. Excessive fine sediment can have widespread impacts on instream ecology (Bilotta and Brazier, 2008; Jones *et al.*, 2011; Murphy *et al.*, 2015). Fine sediment is now classified as a diffuse pollutant in Europe under the WFD and is a contributory factor to hydromorphological degradation, one of the main reasons for failure to achieve WFD obligations across Europe (European Environment Agency, 2012). Within England, the Environment Agency's national risk assessment shows that the numbers of water bodies at risk of failing to reach 'good' status by 2015 due to sediment pressure (primarily from agricultural sources) has increased from 13% to 23%, and there has been significant investment in control measures (Environment Agency, 2015). Our results emphasise the importance of integrating assessments of invasive non-native species impacts on sediment loadings in order to improve the effectiveness of such measures and support prioritisation of efforts and investment. Furthermore, since bank material delivered through burrowing will comprise minerogenic particles, organic material and fine sediment-associated nutrients and contaminants, there may be further potential implications for water quality depending on point and diffuse sources in different catchments (Walling *et al.*, 2003).

6. CONCLUSION

The impacts of invasive non-native species on the physical river environment remain largely unquantified, despite the potential for catastrophic impacts from some species. This paper provides the first multi-catchment analysis of invasive non-native crayfish burrowing and reveals that the majority of invaded systems were impacted by burrowing to some degree. The distribution of burrows was patchy in spatial organisation but can be locally intensive, and was largely determined by local bank properties although it is likely that other factors such as population density, predation and availability of alternative shelter also play a role. Burrow excavation alone delivers a considerable amount of sediment to river systems, exceeding 3 t km^{-1} burrowed bank. Furthermore, burrowing is associated with bank profiles typical of eroding cliffs and outer meander bends, and hence is occurring on banks that are either actively eroding or exposed to fluvial action and/or mass failure processes. This provides the first quantitative evidence that river bank burrowing by invasive non-native crayfish may cause or accelerate river bank instability and erosion in invaded catchments beyond the scale of individual burrows.

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Figure 1 (a) Map of the research catchments showing observations of invasive crayfish species and surveyed reaches. Data courtesy of the NBN Gateway with thanks to all the data contributors (https://data.nbn.org.uk/Datasets). The NBN and its data contributors bear no responsibility for the further analysis or interpretation of this material, data and/or information. Reaches with burrows were surveyed for the bank section analysis (crosses). (b) Schematic representation of bank section sampling design for a representative 500m reach.

Figure 2 Example indicators of bank erosion on the River Mole: (a) undercut exposed bank indicating fluvial erosion and (b) slumped material indicating mass failure.

Figure 3 Burrowing characteristics by river: (a) number of reaches with and without observed burrows (n=103), (b) % impacted bank length for reaches with burrows (n=69), and burrow metrics (no. burrows, impacted length and density) assessed at the bank section scale (c-e; n = 245).

Figure 4 Differences in selected biophysical properties between (a-c) reaches with burrows observed (grey) and not observed (white) and bank sections (d-h) with burrows observed (grey) and not observed (white).

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Table 5 Logistic regression model used to predict occurrence of crayfish burrows at the bank section scale

Table 6 Estimated volume of sediment excavated by crayfish burrowing based on field survey

Figure 1

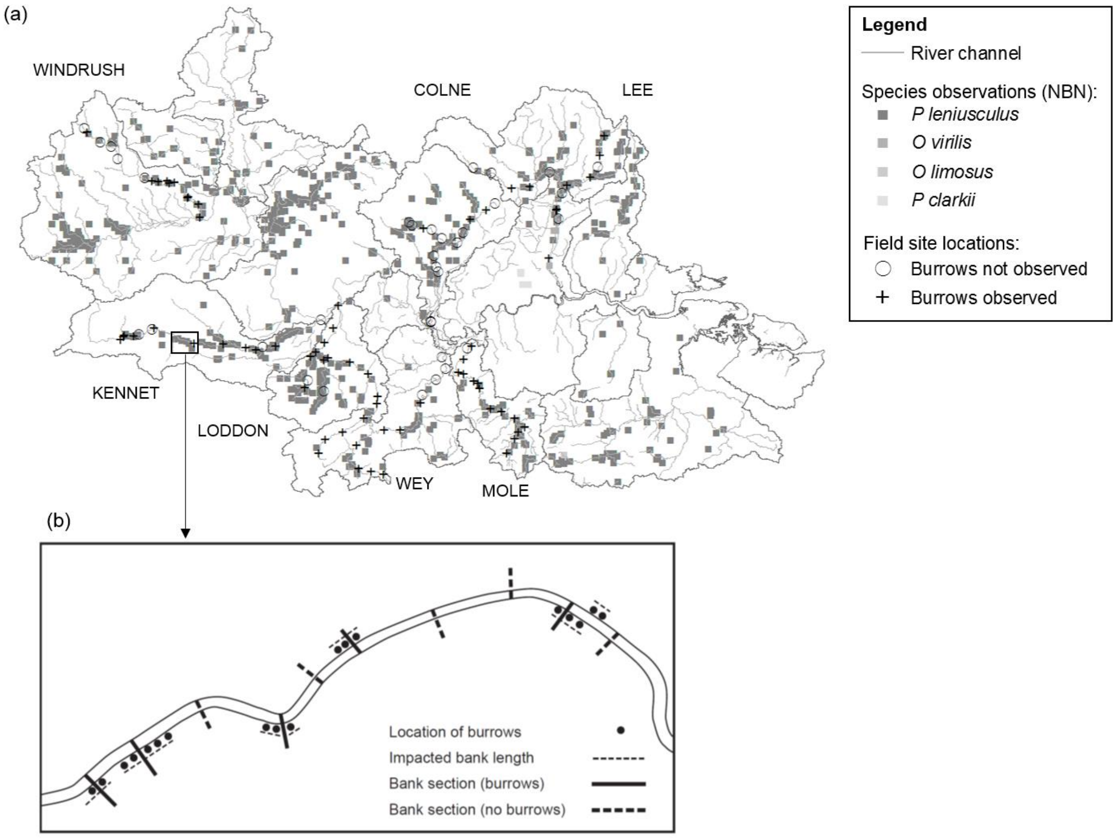

(a)
WINDRUSH
COLNE
LEE
KENNET
LODDON
WEY
MOLE
Legend
River channel
Species observations (NBN):
P leniusculus
O virilis
O limosus
P clarkii
Field site locations:
Burrows not observed
Burrows observed
(b)
Location of burrows
Impacted bank length
Bank section (burrows)
Bank section (no burrows)

Figure 2

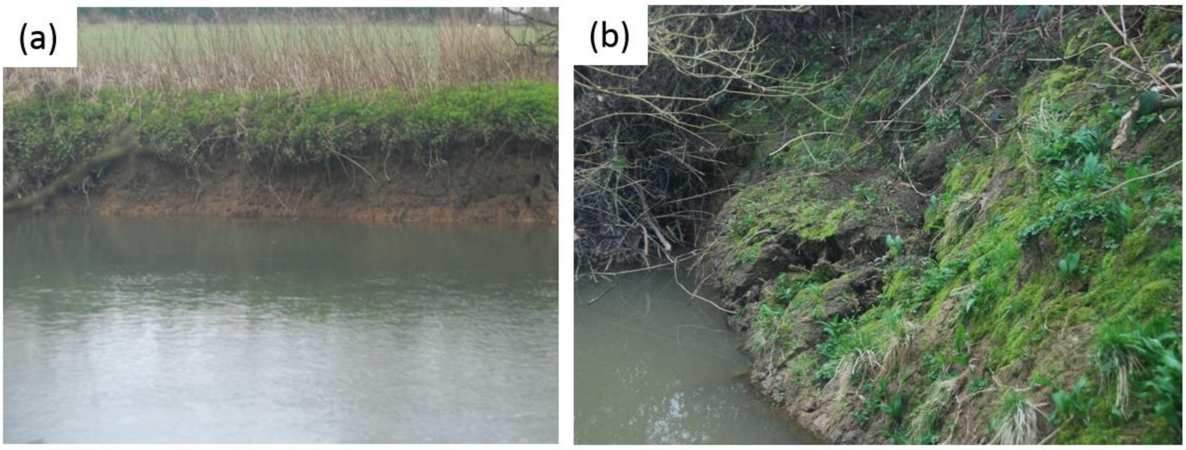
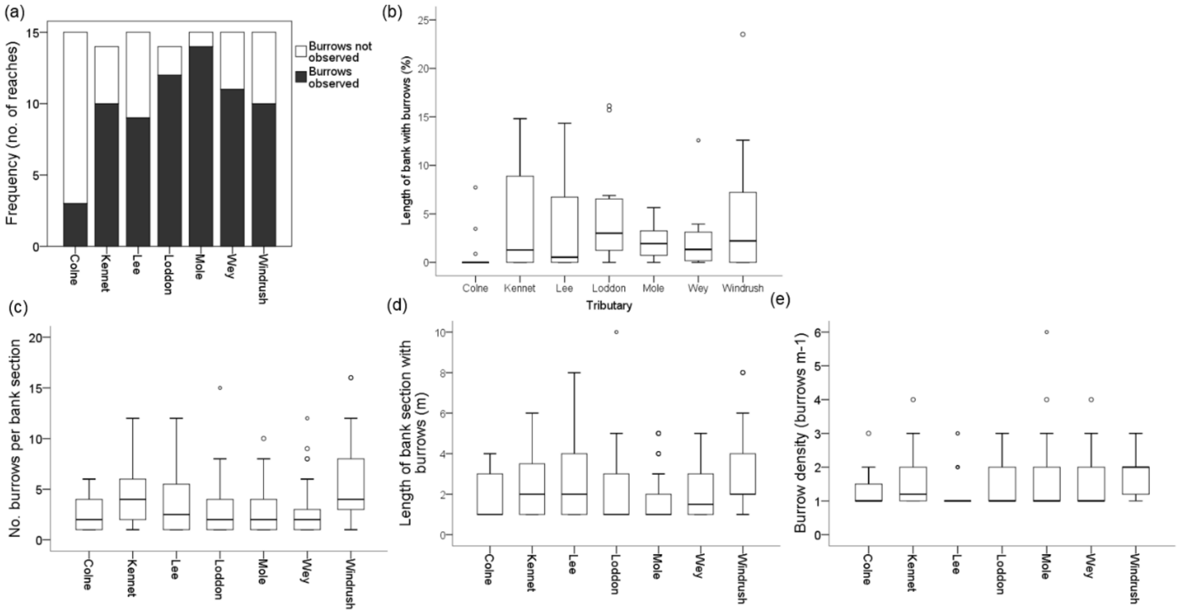


Figure 3.



(a)
Frequency (no. of reaches)
Burrows not observed
Burrows observed
Colne
Kennet
Lee
Loddon
Mole
Wey
Windrush
(b)
Length of bank with burrows (%)
Tributary
(c)
No. burrows per bank section
(d)
Length of bank section with burrows (m)
(e)
Burrow density (burrows m-1)

Figure 4

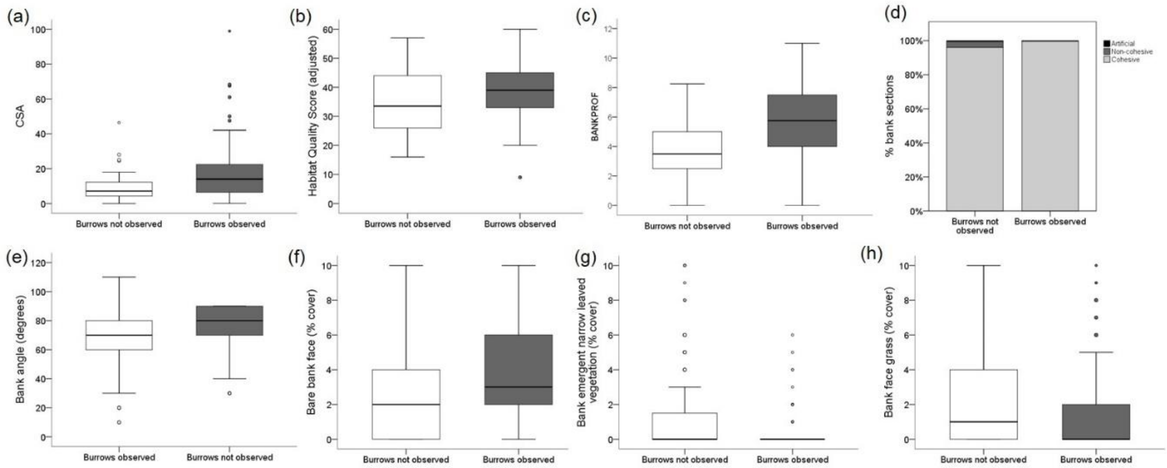
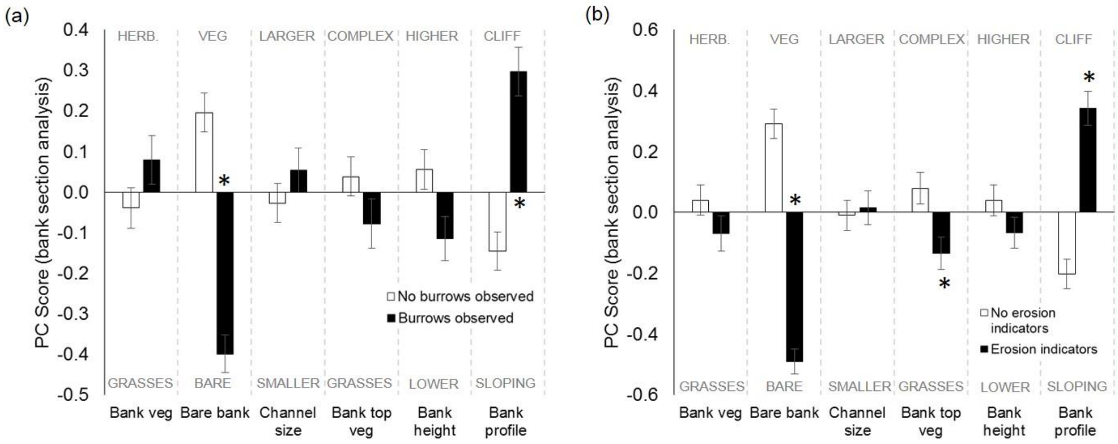
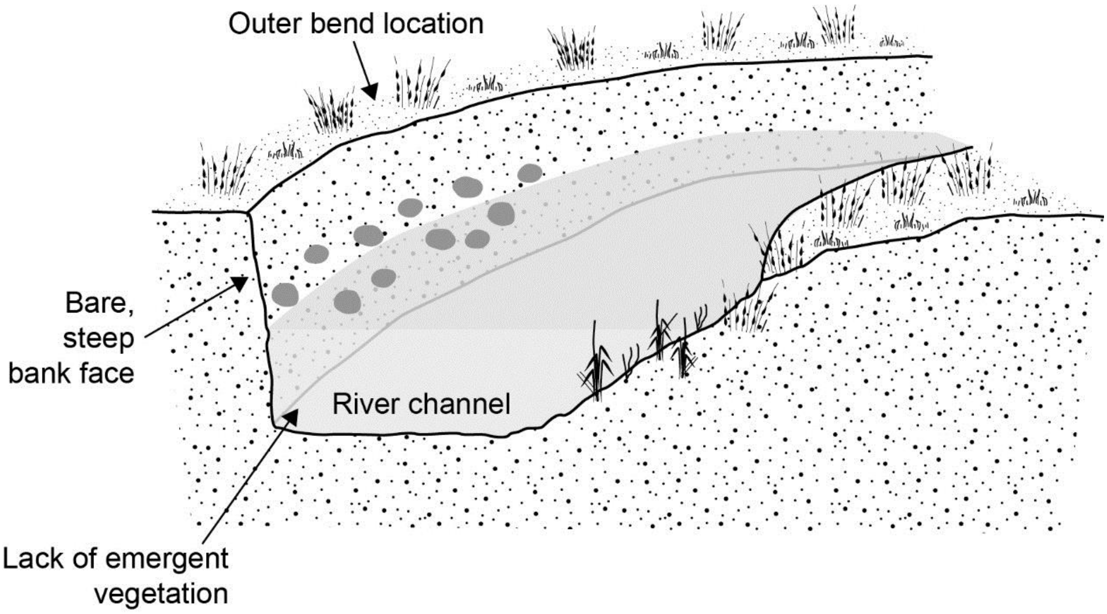

(a)
CSA
Burrows not observed
Burrows observed
(b)
Habitat Quality Score (adjusted)
Burrows not observed
Burrows observed
(c)
BANKPROF
Burrows not observed
Burrows observed
(d)
% bank sections
Artificial
Non-cohesive
Cohesive
Burrows not observed
Burrows observed
(e)
Bank angle (degrees)
Burrows observed
Burrows not observed
(f)
Bare bank face (% cover)
Burrows not observed
Burrows observed
(g)
Bank emergent narrow leaved vegetation (% cover)
Burrows not observed
Burrows observed
(h)
Bank face grass (% cover)
Burrows not observed
Burrows observed

Figure 5



(a)
PC Score (bank section analysis)
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
HERB.
VEG
LARGER
COMPLEX
HIGHER
CLIFF
GRASSES
BARE
SMALLER
GRASSES
LOWER
SLOPING
No burrows observed
Burrows observed
Bank veg
Bare bank
Channel size
Bank top veg
Bank height
Bank profile
(b)
PC Score (bank section analysis)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
HERB.
VEG
LARGER
COMPLEX
HIGHER
CLIFF
GRASSES
BARE
SMALLER
GRASSES
LOWER
SLOPING
No erosion indicators
Erosion indicators
Bank veg
Bare bank
Channel size
Bank top veg
Bank height
Bank profile

Figure 6



Outer bend location
Bare, steep bank face
River channel
Lack of emergent vegetation

Table 1. RHS-based variables and indices used to characterise reaches. Unless specified, indices were derived from RHS data and based on Emery et al. (2004).

	Variable / Index	Source data/reference and description
Landscape indices	Site altitude (m)	Calculated from Digimap (2015), indicates reach-scale energy conditions
	Slope (m/m)	
	TSPI (m^3m^{-1})	Total Stream Power Index (CSA x slope)
	CSA (m^2)	Cross sectional area indicating channel dimensions
Local physical indices	SEDCAL	Bed sediment calibre, indicates availability of larger clasts (shelter), bed stability, hydraulic environment
	BANKCAL	Bank sediment calibre, indicates characteristics of bank material into which burrows are dug.
	BANKPROF	New bank profile index computed using RHS data: (V + VT + S + G + C + B)/6 Where: V (Vertical) = LB*5 + RB * 5; VT (Vertical with toe) = LB *4 + RB * 4; S (steep > 45°) = LB*3 + RB*3; G (Gentle) = LB*2 + RB*2; C (composite) = LB*1+RB*1; B (natural berm) = LB*1+RB*1 and LB/RB = 0 (absent), 1.5 (present) or 3 (extensive).
	FLOW	FLOW = (1*NP + 2*SM + 3*UP + 4 *RP + 5 *UW + 6 *BW + 7 *CF + 8 *CH + 9*FF) / (NP + SM + RP + UW + BW + CF + CH + FF). Where: NP (no perceptible flow), SM (smooth flow), UP (upwelling), UW (unbroken standing waves), BW (broken standing waves), CF (chaotic flow), CH (chute flow) and FF (free fall represent the number of transects allocated to each flow type.
Ve	INCHANVEG	In channel vegetation index, indicates cover/complexity of

		instream vegetation types providing habitat, food, shelter.
	BANKVEG	Bank vegetation index, indicates complexity of bank vegetation and hence cover/accessibility at the bank face.
	TTS	Total Tree Score, indicates complexity of the riparian zone and hence availability of cover/ allochthonous inputs.
Habitat indicators	HMS	Habitat Modification Score (HMS) indicates level of disturbance to river habitat by channel and bank modifications. Provided in RHS database.
	HQA	Habitat Quality Assessment (HQA) overall quality of habitat in the reach, including presence of diverse habitat features. Provided in RHS database.

Table 2. Variables recorded at the bank section scale. Turbidity and water depth limited in-channel observations at a large number of bank sections.

	Variable name	Variable description (units/categories)
Bank characteristics and vegetation	Bank material	Artificial (1), non-cohesive (2), cohesive (3)
	Bank angle (°)	Angle of the bank face
	Planar angle (°)	Curvature of river meander measured between observation point and points on the same bank five river widths upstream and downstream (+ for outside of meander bend and – for inside of bend)
	Exposed bank height (m)	Above the water surface, to indicate bank height above low flow water level (and incision).
	Bank emergent broad leaved vegetation	1% cover of vegetation adjacent to bank toe.
	Bank emergent narrow leaved vegetation	% cover of vegetation adjacent to the bank toe. Includes Reeds, sedges, rushes, grasses, horsetails
	Bank face vegetation categories: bare, grasses, herbaceous, shrubs trees	% cover of for each separate category (to nearest 10%).
	Bank top vegetation categories: bare, grasses, herbaceous, shrubs, trees	% cover for each separate category (to nearest 10%)

Channel characteristics and vegetation	Water width (m)	Measured at water surface under low flow conditions
	Water depth (m)	Under low flow conditions
	Channel substrate	artificial (1), cobble (2), gravel (3), sand (4), cohesive (5)
	Channel large wood	Length (m) of LW (>10cm diameter and >1m length)
	Surface flow type	Flow type (smooth, 1 and rippled, 2).
	Channel vegetation types: emergent broad leaved vegetation, emergent reeds, submerged broad-leaved/fine leaved/linear leaved macrophytes, filamentous algae, floating leaved (rooted)	Presence or absence
Bank erosion	Impacted bank length (m)	Length of bank with features indicative of fluvial bank erosion or mass failure processes (Thorne, 1998).

Table 3. Descriptive statistics for burrow survey metrics

		Mean	Median	Mode	Min	Max	25th	75th
All reaches	Length of bank surveyed (m)	282	270	260	70	800	200	320
Reaches with burrows	Total number of burrows recorded	19	12	1	1	87	4	24
	Length of bank with burrows (m)	13	8	1	1	50	4	18
	Length of bank with burrows (%)	4.9	3.2	-	0.2	23.5	1.3	7.2
Bank sections with burrows	Number of burrows	3.6	3.0	1.0	1.0	16.0	1.0	5.0
	Impacted bank length (m)	2.4	2.0	1.0	1.0	10.0	1.0	3.0
	Burrow density (burrows per m)	1.5	1.0	1.0	1.0	6.0	1.0	2.0

Table 4 Principal Component Loadings for the variables and interpretation of the PCs for reach scale and bank section scale analyses.

PC	Variable loadings	Interpretation	% variance explained
Reach-scale analysis			
PC1	Slope (0.742), CSA (-0.733), FLOW (0.781),	River energy and channel size	20
PC2	BANKVEG (0.628), Total Tree Score (0.552), HQA (0.756), BANKPROF (0.4538), BANKCAL (0.498), HMS (-0.487)	Habitat quality/modification, riparian complexity and bank morphology and material	20
Bank section scale analysis			
PC1	Herbaceous vegetation on bank top (0.839) and face (0.801) and grass on bank top (-0.772) and face (-0.679)	Bank vegetation type	15
PC2	Bare bank face (-0.798), bank face grass (0.500), emergent broad leaved vegetation (0.500), emergent narrow leaved vegetation (0.631)	Availability of bare bank and emergent vegetation	11
PC3	Channel width (0.789), depth (0.814), flow type (-0.704)	Channel size	11
PC4	Bare bank top (0.638), grass on bank top (-0.476), shrubs on bank top (0.569), trees on bank top	Bank top vegetation type	8

	(0.627)		
PC5	Bank height (0.569), shrubs on bank face (0.661), trees on bank face (0.576)	Bank height and tall vegetation coverage	8
PC6	Bank angle (0.608), planar angle (0.711), trees on bank face (-0.458)	Bank profile	7

Table 6 Estimated volume of sediment excavated by crayfish burrowing based on field survey

River	No Burrows	Surveyed bank length (m)	Length impacted (m)	Total volume excavated (L)	Volume excavated per m impacted (L/m)
Colne	41	4710	33	59.2	1.8
Kennet	229	3950	159	330.8	2.1
Lee	187	3280	149	270.1	1.8
Loddon	259	3740	184	374.1	2.0
Mole	129	4500	87	186.3	2.1
Wey	145	4630	109	209.4	1.9
Windrush	309	4230	196	446.3	2.3
Total	**1299**	**29040**	**917**	**1876.3**	**2.0**